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## THE STRENGTHENING SYSTEM IN THE STEM OF MAIZE\*

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### ABSTRACT

The system providing strength to a maize stem is described as consisting of thick-walled, lignified cells located in three distinct stem tissues: hypodermis; peripheral bundle sheaths; and sclerified ground parenchyma. Striking changes occur in the disposition of these tissues from the base of a stem to the apex, which are directly related to the plant's mode of development. Inter-racial differences in amount and arrangement of sclerotic tissue are described, and contrasted with the strengthening systems of *Euchlaena* and *Tripsacum*. WILLIAM H. MURDY, Emory University, Atlanta 22, Georgia.

### INTRODUCTION

The species *Zea mays* is characterized today by an almost overwhelming range of variability; a consequence attributed in part to its unique history in association with ethnic groups of man in the New World, and in part, to former introgression with the genus *Tripsacum* and the present ability to exchange germ plasm with *Euchlaena* (teosinte; a genus of putative hybrid origin between *Zea* and *Tripsacum*).

The concept of race has been advanced as a step toward a natural classification of this variability. Anderson and Cutler (1942), largely responsible for the evolution of this concept, defined a race loosely as a "population of maize plants differing from other groups by a great number of genes and sharing enough characters in common to be easily recognized as a distinct group".

For the past several years, the Rockefeller Foundation in collaboration with Latin American countries has been performing the arduous task of classifying indigenous races of maize in Central and South America. The character of scleroticness, as expressed by features such as stalk stiffness, the coarseness of leaves and cob induration, is one of many polygenic characters by which races of maize have been found to differ. The magnitude of tissue induration is frequently accepted as evidence of teosinte or *Tripsacum* contamination, since highly sclerotic plants often exhibit other plant characters regarded as "tripsacoid" in nature (Wellhausen, 1952). Moreover, segregates from maize-teosinte crosses often

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possess an inordinate degree of tissue induration (Mangelsdorf and Cameron, 1942). Galinat et al. (1956) state that "extensive experiments with maize-teosinte hybrids have demonstrated that genes responsible for lignification occur on many, if not all, of the chromosomes of teosinte".

The character of sclerification, when properly evaluated, should add materially to our knowledge concerning the origin of modern maize and its past and present relationship with *Euchlaena* and *Tripsacum*. The present study was undertaken in order to shed light on the following basic questions: (1) What stem tissues become sclerified to make up the strengthening system and how do these tissues differ in amount and arrangement from the base of a stem to its apex? (2) What is the range of variability within and between races of maize in respect to the strengthening system? (3) What relationship exists between the strengthening system of maize and that of *Euchlaena* and *Tripsacum*?

One of the foremost requisites of good breeding stock is an ability to stand up well and contribute a fair share of stalk-stiffness in crosses. Several anatomical studies, based on the lower internodes of inbred lines, have established a correlation between lodging resistance and the nature of sclerotic tissue (Magee, 1948; Hunter and Dalbey, 1937). The results of these investigations are valuable to the corn breeder, but have only an indirect bearing on the nature of sclerotic, strengthening systems in vigorous open-pollinated races.

#### MATERIALS AND METHODS

Six maize races were selected from the "Standard Exotics" described by Anderson and Brown (1951), which represent the extremes of variation in *Zea mays* growable in the corn belt. Many plants of each race were grown under essentially uniform field conditions at the Pioneer Hi-Bred Corn Company, Des Moines, Iowa. Following is a brief description of each race.

Gourdseed (Brown and Anderson, 1948)—An old southern dent variety typical of the kind of maize commonly grown in southeastern United States in colonial times. This particular stock was collected by Dr. W. L. Brown in 1946 at Grapevine, Texas. Plants are generally tall, having many internodes, few tillers, and greatly condensed ears and tassels. Chromosome knob numbers medium high (5-7); plants mature slowly (approximately 94 days from planting to silk in Iowa).

Northern flint (Brown and Anderson, 1947)—Representative of the maize once grown almost exclusively in the northern and eastern sectors of the United States until superseded by early corn-belt varieties. Plants vary somewhat throughout their range, but share many features in common including low chromosome knob numbers (0-2), eight-rowed ears, few, but long internodes (those above the ear not decreasing in length as in the case of Gourdseed), several tillers shorter in height than the main stem, and a rapid growth rate (from planting to silk in Iowa takes approximately 66 days).

Argentine pop (Anderson and Brown, 1951)—A small-eared, prolific pop corn race of Paraguay and Argentina. Unlike the other five races, Argentine pop has not likely been contaminated by either North American *Tripsacum* or teosinte. Furthermore, its ear is closest to the concept of prehistoric South American maize



based on archeological evidence. It grows slowly in Iowa and at maturity consists of a main shoot with many short internodes relatively equal in length, plus a few tillers shorter than the main culm. Planting to silk requires approximately 105 days.

Chapalote (Wellhausen, 1952)—A pop corn race grown in the coastal lowlands of northwestern Mexico. Plants are "tripsacoid" in appearance in the possession of several long, ear-bearing tillers approaching in height the main shoot, long internodes, and long narrow leaves. Wellhausen classified this race as a primitive, indigenous pop corn with little evidence of teosinte contamination. Chromosome knob number is variable; the average is approximately six. About 90 days are required from planting to silk in Iowa.

Papago (Anderson and Cutler, 1942)—Seed of this race was obtained from the Papago Indians in the desert south of Tucson, Arizona. It is typical of the maize grown by desert-dwelling Indians and similar to archeological maize grown by the prehistoric Basketmakers—the first agriculturalists of this region to leave a record (Anderson and Blanchard, 1942). Its habit resembles that of Chapalote; long ear-bearing tillers, long internodes, and long narrow leaves. Chromosome knob number is medium high and growth rate quite rapid (approximately 77 days from planting to silk in Iowa).

Zapalote chico (Wellhausen, 1952)—An extremely sclerotic race grown in the coastal lowlands of southern Mexico. Plants are coarse and indurate, lack tillers, and have many short internodes above the ear. Chromosome knob number is high (12–16) and Wellhausen considers this race to be highly contaminated with teosinte germ plasm. It matures rapidly in its native habitat and is comparatively independent of day length when grown in Iowa. Planting to silk requires approximately 81 days.

Six plants of Florida teosinte (*Euchlaena mexicana*), from a commercial source, were used in this study; two were grown in Iowa and four in Florida. Plants from two separate clones of *Tripsacum dactyloides* were sampled; one growing in Iowa and the other located in St. Louis, Missouri. A single plant of *Tripsacum lanceolatum* collected in Guatemala by Dr. E. Anderson was also included in this study.

Just after anthesis, 15 plants of each maize race were selected in an attempt to adequately sample the range of morphological variability within races. Plants were collected when completely mature and subsequently subjected to morphological and anatomical analysis. In making anatomical sections of desiccated stems, internodal discs about 2 cm. long were boiled in water, with aerosol added, for approximately 4–5 hours; placed in 50 percent alcohol overnight; sectioned with a sharp razor; stained with safranin and fast green; and permanently mounted in piccolyte, a synthetic mounting medium.

#### MATURATION OF A MAIZE STEM

The stem of maize can be looked upon as a series of alternating segments, or phytomers (Evans and Grover, 1940). Each phytomer is made up of an internode, with a leaf at its upper end and a bud at its base. Final maturation of a phytomer begins in the leaf blade, passes down the leaf sheath and finally down the internode



below. Successive phytomers, however, mature acropetally up to, but not including, the tassel peduncle, which together with its tassel does not await the ascending wave of maturation, but matures relatively early at a time when the internodes immediately below are still immature. Normally there is no leaf associated with the tassel peduncle, thus, internodal tissue maturation begins in the upper portion of this internode. By measuring internode lengths of genotypically uniform hybrid plants at various stages of maturity, one is able to obtain a picture of the ontogenetic pattern of stem development (fig. 1). Note the plant examined ten weeks after planting; it is still relatively immature, nevertheless, the leafless peduncle is already 11 cm. long, almost half its assumed maximum length, while the two internodes immediately below, associated with leaves, are merely 2 cm. in length, only one-ninth their assumed maximum length at maturity.

A similar pattern of maturation was reported by Prat (1935) for stems of *Secale cereale*. He noted that the terminal internodes bearing the inflorescence elongated more rapidly than the subterminal internode. By subjecting these two internodes to mechanical stress, he found the uppermost to be more resistant. He concluded that rapid maturation accompanied rapid elongation and that both processes occurred faster in the terminal internode than in the one below.

It is likely that the maturation of a maize stem conforms to a pattern widespread in the Graminae. Knowledge of this pattern is essential to an understanding of maize stem anatomy, for the rate at which an internode grows and matures has a direct bearing on its internal structural features.

#### STRENGTHENING TISSUES IN A MAIZE STEM

In herbaceous monocots generally, mechanical stem strength is provided by thick-walled sclerotic tissue. The process of cell sclerification entails the deposition of a thick, cellulosic secondary wall and subsequent impregnation of primary and secondary walls with lignin. Tissues that contribute most to the strength of a maize stem can be classified in three categories: (1) sclerenchyma associated with vascular bundles; (2) hypodermal sclerenchyma; (3) sclerified parenchyma.

*Vascular bundle sclerenchyma.* A maize stem in cross-sectional view (plate VI, D) shows a scattered arrangement of vascular bundles surrounded by parenchymatous ground tissue. Those bundles near the periphery of the stem are crowded, small and generally provided with heavy sclerotic sheaths, whereas the more central ones are widely-spaced, larger in size, and lack massive sheaths. The presence of two distinct vascular systems in maize has previously been reported. Both Esau (1943) and Cutler and Cutler (1948) reported two systems in the stem. The latter authors referred to the outer system as the "peripheral" and the inner as the "central". Two quite dissimilar systems have also been noted in the ear (Lenz, 1948; Laubengayer, 1949; Reeves, 1950) and tassel (Kumazawa, 1940).



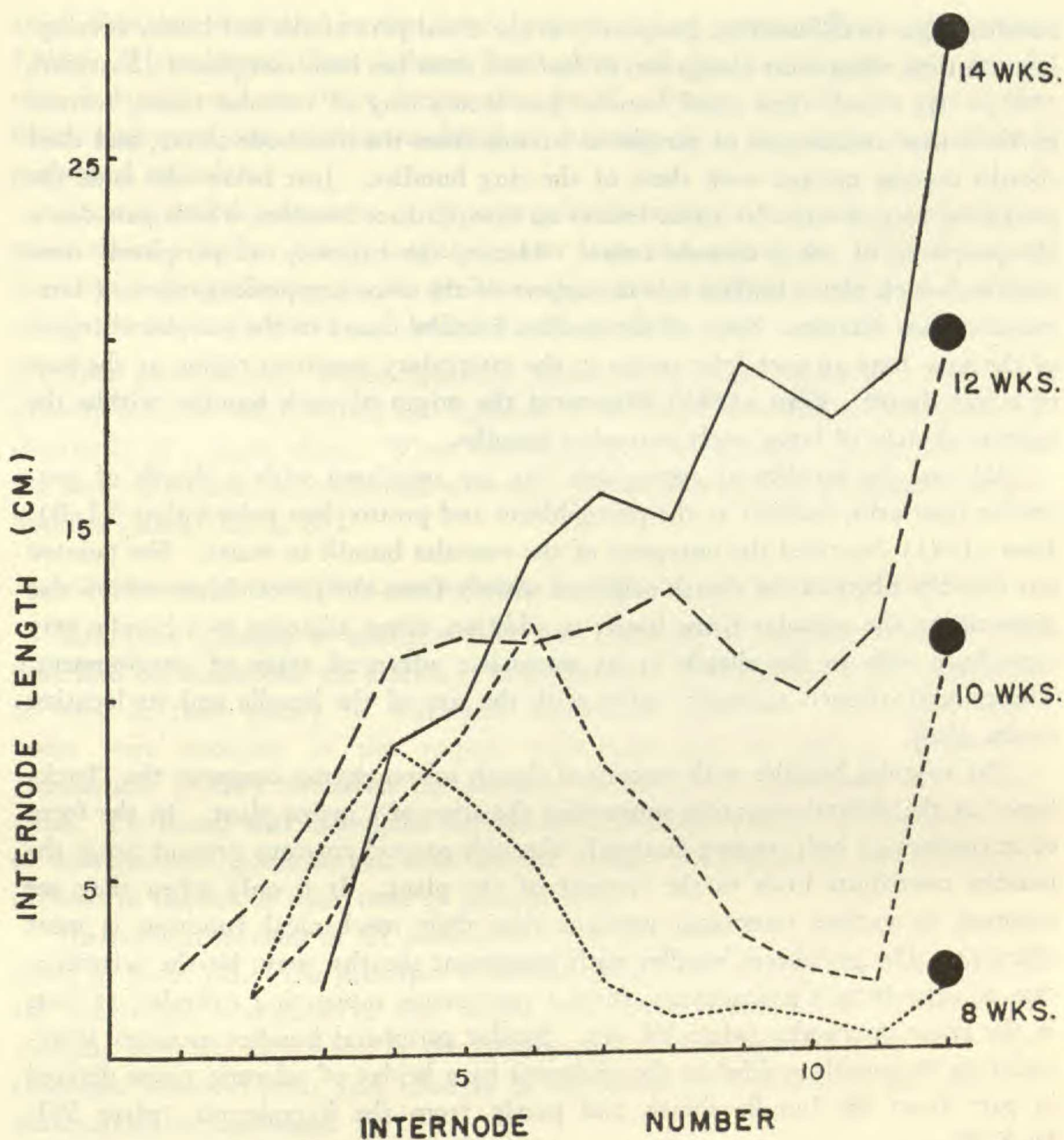


Fig. 1. Internode diagrams of genotypically identical plants measured at intervals of 8, 10, 12, and 14 weeks after planting. Successive stem internodes elongate acropetally except for the tassel peduncle.

The leaves of maize are vascularized by large, early-maturing bundles and smaller late-forming bundles which alternate with the larger ones. At a node, the large leaf bundles pass some distance into the stem at a right angle before assuming a vertical or oblique course down through the internode below. Ontogenetically, the large bundles originate at the node and simultaneously differentiate in two directions; up into the leaf and down through the internode before either of these organs have completed their elongation. Only when acropetal differentiation of these large bundles reaches the tip of the leaf blade, do the small alternating



bundles begin to differentiate basipetally in the distal part of the leaf blade, developing at a time when most elongation of leaf and stem has been completed (Sharman, 1942). At a node these small bundles pass into a ring of vascular tissue, formed by the lateral anastomosis of peripheral strands from the internode above, and their sheaths become merged with those of the ring bundles. Just below the node the peripheral ring of vascular tissue breaks up into distinct bundles, which pass down the periphery of the internode below. Hence, the majority of peripheral stem bundles, which play a leading role in support of the stem, are prolongations of late-maturing leaf bundles. Some of the smallest bundles found in the peripheral region of the stem have an even later origin in the intercalary meristem region at the base of a leaf sheath. Esau (1943) illustrated the origin of such bundles within the massive sheaths of large, early-maturing bundles.

All vascular bundles of appreciable size are associated with a sheath of protective fiber cells, heaviest at the protophloem and protoxylem poles (plate VI, B). Esau (1943) described the ontogeny of the vascular bundle in maize. She pointed out that the fibers of the sheath originate mainly from the procambium which also gives rise to the vascular tissue itself; in addition, tissue adjacent to a bundle may contribute cells to the sheath in its somewhat advanced stage of development. The amount of such accretion varies with the size of the bundle and its location in the plant.

The vascular bundles with associated sheath sclerenchyma comprise the "backbone" of the skeletal structure supporting the stem of a maize plant. In the form of strengthening rods passing discretely through parenchymatous ground tissue the bundles contribute little to the support of the plant. It is only when they are arranged in various structural patterns that their mechanical function is most effective. The peripheral bundles with prominent sheaths, may, by the sclerification of inter-bundle parenchyma, form a continuous supporting cylinder, at least in the lower internodes (plate VI, A). Similar peripheral bundles in upper internodes are frequently welded to the epidermis by a bridge of sclerotic tissue derived in part from the bundle sheath and partly from the hypodermis (plate VII; D, E, F).

*Hypodermis.* Immediately beneath the epidermis of a maize stem is a zone of thick-walled, elongate fiber cells (plate VI, A). This tissue, commonly known as a hypodermis, is lacking or poorly developed in lateral and foliar organs. Frequently the hypodermis is very thick in its radial dimension and makes a substantial contribution to the strength of certain parts of the stem.

Ontogenetically, the subepidermal meristematic cylinder which gives rise to the hypodermis probably originates from the "flank meristem" of Ledin (1954). Popham (1951) refers to this histogen as a peripheral meristem forming a cylinder between the protoderm, which gives rise to the epidermis, and central meristem, which develops into pith and procambial strands. In ontogeny, parenchyma cells underlying the epidermis undergo longitudinal divisions and as the internode elongates, these initials do not undergo transverse division, but grow rapidly in the



axial direction resulting in the development of long narrow fibers (Hayward, 1938). Hypodermal fibers isolated from plants of the race Papago average 1.2 mm. in length and are  $100\times$  longer than broad. During growth, the tips of the fibers push past one another resulting at maturity in a very strong non-storied peripheral cylinder.

Accentuated development of hypodermal sclerenchyma is found just above the point where a leaf or lateral branch departs from the main stem. This fact may have a significant bearing on the problem of intense sclerification of the cob rachis where the internode above each lateral branch (spikelet pair) is greatly abbreviated.

*Sclerified parenchyma.* Parenchymatous tissue in the outer region of a stem frequently becomes thick-walled and lignified to an extent that differs greatly among internodes of a single plant. When well-developed, the sclerotic parenchyma takes the form of a thick, subepidermal, sclerotic cylinder pervaded by peripheral vascular bundles (plate VII; A, B).

#### CHANGES IN THE STRENGTHENING SYSTEM OF AN INDIVIDUAL STEM

Structural changes in anatomy from one internode to another have not been described for maize, but are known in other grasses. Prat (1935) found internodes to vary in their ability to withstand mechanical pressures. The lower internodes were strongest in this respect with resistance diminishing acropetally. Athanassoff (1928) described the anatomy of successive internodes of a wheat culm. He found that internodes differed in the relative amount and arrangement of sclerenchyma, parenchyma, and vascular tissue. He also noted that internodes differed in respect to their time of maturation.

Anatomical sections of six internodes from the stem of a single plant are pictured in plate VII. The principal structural differences among internodes include the following: variation in size, shape, and sheath development of peripheral vascular bundles; differences in the relationship of these outer bundles with subepidermal sclerenchyma; and, changes in the extent of hypodermis and sclerified parenchyma development.

*Peripheral vascular bundles.* The peripheral bundles are very small in the lowermost internode (plate VII, A), but increase in size acropetally. In the internodes below the ear (plate VII; A, B, C) peripheral bundle sheaths, though massive, show very little centrifugal development, and between sclerenchyma at the proto-phloem end of the bundles and sclerenchyma of the hypodermis is a zone of thin- or thick-walled parenchyma. Peripheral bundles in the internodes above the ear (plate VII; D, E, F) are large in size and rhomboid in shape. These bundles have a much greater development of sheath sclerenchyma at the proto-phloem pole which, being confluent with the hypodermis, results in the formation of sclerotic "bridges" connecting the peripheral bundles to the epidermis.

The small, peripheral bundles in the lower internodes (plate VII; A, B) evidently matured after these internodes had ceased to elongate. They have little protophloem and protoxylem and are relatively unstretched, as evidenced by the



lack of a protoxylem lacuna (Esau, 1943). Their complete dissociation from the hypodermis and sub-epidermal parenchyma infers that their development in the internode occurs after these outer stem tissues have matured. In the internode just below the lowest ear (plate VII, C) peripheral bundles are somewhat larger than in lower internodes. In addition, they possess protoxylem and the middle bundle is somewhat stretched. Therefore, up to this point, there is an acropetal narrowing of the time lag between the maturation of the outer internodal tissues and the peripheral bundles. From the next internode on into the tassel the anatomy of the stem undergoes a striking change (plate VII, D). In these upper internodes, peripheral bundles differentiate prior to the completion of internode elongation and at a time when the outer tissues of the internode are still immature and capable of further division and elongation. As a result, these bundles are large, with well developed protoxylem and protophloem, and a large protoxylem lacuna. Moreover, bundle sheaths are well developed at the protophloem pole and confluent with hypodermal sclerenchyma. Except for size, the peripheral bundles in the peduncle and tassel (plate VII; E, F) are comparable to those of the internodes immediately below and are similarly bridged to the epidermis.

The structural variation of vascular bundles in the corn stem described above is attributable to differences in the relative period of development and maturation of outer stem tissues and the vascular bundles descending through them from leaves above. Starting with the lowermost internodes where the peripheral bundles develop some time after the completion of internode elongation, there is a gradual change in this relationship whereby the development and maturation of the two tissues is progressively more closely approximated. At a point where the lowermost ear is borne, the development and maturation of the two tissues is coincident. Sharman (1943) has pointed out that the time taken for the internode to complete its development increases with the maturity of the plant. He noted that "in the upper internodes there may be a lapse of four or more plastochrones between the full expansion of the lamina and internode." In other words the development and maturation of leaves with their included vascular strands, occurs at a fairly uniform rate acropetally, whereas the maturation of tissue in successively higher internodes progressively slows down.

An internode pattern of this plant (fig. 4, lower right) shows that the lower internodes (aside from the first two above the ground), which on the basis of anatomy were found to mature rapidly, are elongate, whereas the slower-maturing, upper internodes have relatively short lengths. Consequently, the changes in the length of internodes coincides with the changes in structural anatomy and both reflect the particular growth behavior characteristic of this plant.

*Hypodermis.* The greatest development of hypodermal sclerenchyma occurs in the middle internodes of the plant (plate VII; C, D), diminishing in extent below (plate VII; A, B) and above, where it is found only opposite bundles in peduncle and tassel internodes (plate VII; E, F). The lower internodes and tassel mature more rapidly than internodes between and those just beneath the peduncle are the slowest to mature. It is precisely in these short, upper internodes, having the slowest rate of maturation, that the hypodermis has its greatest development.



*Sclerified parenchyma.* In the upper internodes intervening parenchyma between peripheral bundles is firm, but relatively thin-walled and unligified. Intense sclerification of ground parenchyma occurs in internodes quite low on the plant (plate VII; A, B). The lower internodes are the earliest to originate and have a longer period of time to deposit cell wall material. In addition, there is a great basipetal flow of sugar through these lower internodes especially in the early stages of the plant's growth. The upper internodes have a longer period to differentiate fiber cells, but a shorter period for these cells to deposit cell wall material prior to final desiccation. Furthermore, after fertilization of the ear a great amount of sugar is channeled into the developing kernels causing a drain on the availability of sugars required for the synthesis of cellulose in late-developing internodes.

#### RACIAL VARIATION IN THE STRENGTHENING SYSTEM OF MAIZE

*Hypodermis.* In all races examined (except Argentine pop) hypodermal tissue develops to its greatest extent in the upper stem internodes between ear and tassel. It is suggested that prolonged activity of the peripheral meristem in these upper, slower-maturing internodes results in the differentiation of a great number of hypodermal fiber cells prior to tissue maturation. Races differ, however, in the extent of hypodermal tissue development, which may in part result from a dissimilarity in growth behavior. For example, plants of the race Gourdseed consistently have a thicker hypodermis (greater radial number of fiber cells) than do plants of the race Northern flint (plate VIII; B, D). As a race, however, Gourdseed is characterized by having a slow rate of growth and a series of short slow-maturing internodes above the ear shoot—the region of greatest hypodermal development in all races. Northern flint plants, on the other hand, have a rapid growth rate and the upper internodes are long and relatively quick to mature. Therefore, when comparing the potential ability of these two races to produce hypodermal sclerenchyma, their respective growth patterns must not be overlooked. Although in most races the upper internodes invariably mature more slowly than middle and lower ones, the race Argentine pop is characterized by a very uniform rate of growth resulting in all internodes being short and relatively slow to mature. In plants of this race middle internodes of the stem show the greatest extent of hypodermal development (plate IX, B).

Growth rate does not wholly account for the hypodermal differences observed among races. Papago, the race with the thickest hypodermis (plate VIII, A), is one of the most rapid to mature. In this race, however, the unusually heavy hypodermis is associated with deep-lying peripheral vascular bundles and both features may have definite selective value for such a semi-xerophytic race in diminishing the extent of water loss from stem tissues.

The amount of hypodermal tissue development in plants of a particular race is fairly uniform. Where intra-racial differences do occur, they are accompanied by changes in the overall scleroticness of the plant. When the width of the hypo-



dermal zone is measured in the internode of its greatest development, races of maize analyzed line up from greatest to least in the following manner: Papago (plate VIII, A); Gourdseed (plate VIII, B); Zapalote chico (plate VII, D); Chapalote (plate VIII, C); Argentine pop (plate IX, B); Northern flint (plate VIII, D).

Hypodermal tissue is not a prominent feature in the stems of teosinte plants examined (plate VIII, E). *Tripsacum* likewise lacks an appreciable development of continuous hypodermal tissue. The strengthening system of *Tripsacum*, however, is characterized by separate, peripheral strands of procambial tissue which at maturity form sclerotic connections between peripheral vascular bundles and epidermis. Thin-walled chlorenchymatous tissue lies between adjacent girders.

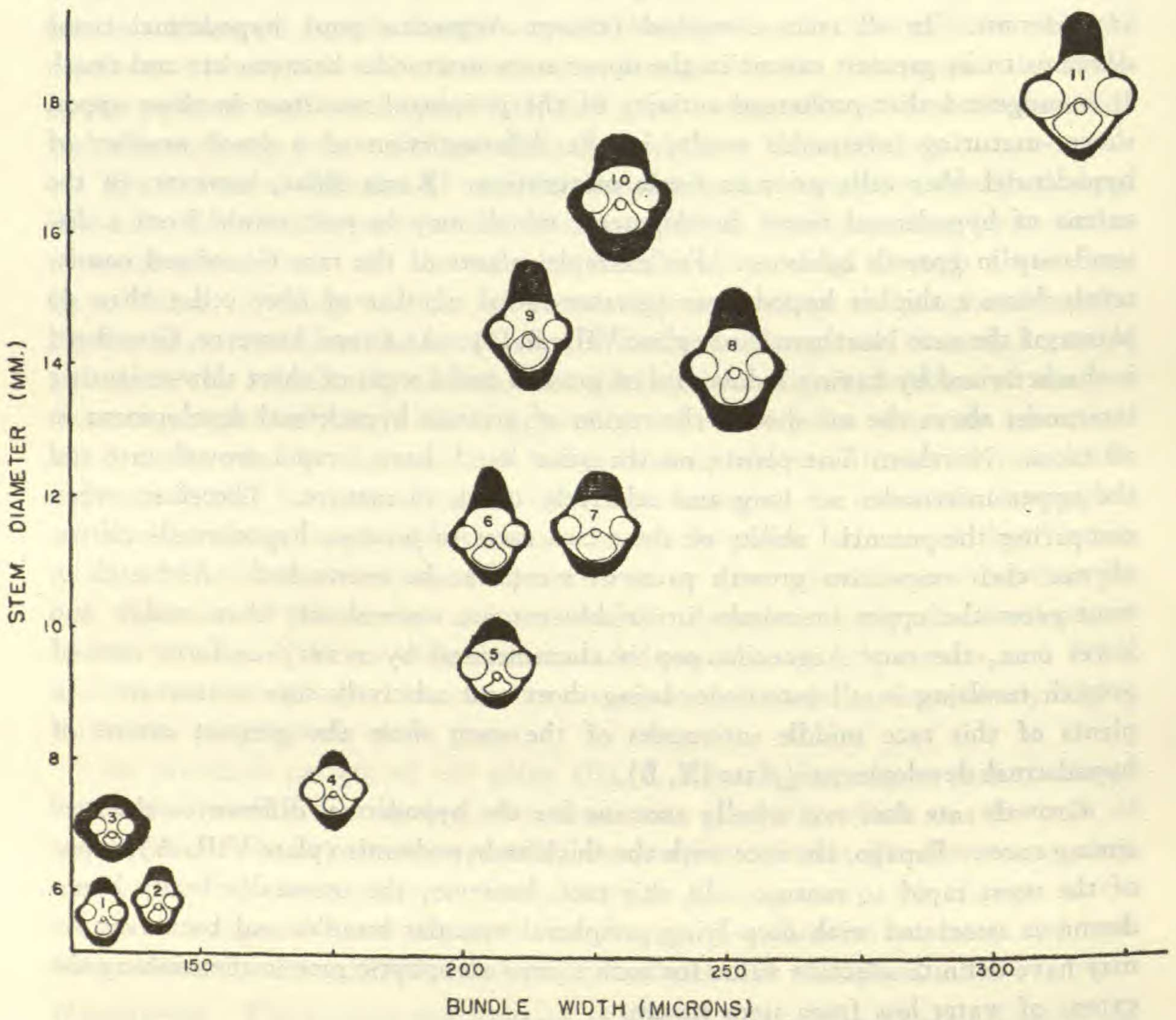


Fig. 2. Pictorialized scatter diagram to show the relationship of bundle width to stem diameter and amount of bundle sheath sclerenchyma for six races of maize plus teosinte and two species of *Tripsacum*. 1, *Tripsacum dactyloides*; 2, Teosinte grown in Florida; 3, *Tripsacum lenceolatum*; 4, Teosinte grown in Iowa; 5, Argentine pop; 6, Gourdseed; 7, Chapalote; 8, Northern flint; 9, Zapalote chico; 10, Papago; 11, Gourdseed (extreme plant).



*Vascular bundles.* The vascular bundles found in any cross section of a corn stem vary in size, shape, and also in their amount of associated sheath sclerenchyma (plate VI, D). Just inside the outer ring of heavily sclerotic bundles is a zone of strands, intermediate in character between the small, often reduced peripheral strands and the large, greatly stretched central ones. This ring of bundles is most easily discerned in the upper internodes of a corn stem and within a particular internodal cross section bundles are remarkably uniform in all their features. Determinations of bundle size were carried out on five such bundles (one appears on plate VI, B) from the fourth internode below the peduncle in each plant studied. Bundle size refers only to the dimensions of the vascular tissue within the bundle sheath.

Vascular bundle size varies somewhat among plants of a single race, but to a greater extent from plants of one race to those of another. Nevertheless, in both instances there exists a strong correlation between the diameter of a particular internode and the size of its contained bundles. The relationship of bundle size to stem diameter for five races of maize plus teosinte and two species of *Tripsacum* is diagrammed in fig. 2. Each symbol represents the average bundle dimensions of a race with the relative amount of sheath sclerenchyma in black. The races Papago (10), Northern flint (8), Zapalote chico (9), and most Gourdseed plants (6) show a heavy development of sheath sclerenchyma in proportion to bundle size, especially when compared with Chapalote (7), Argentine pop (5), and teosinte (4). Relative to bundle size, sheath sclerenchyma is weakly developed in teosinte, greatly developed in *Tripsacum dactyloides* (2), and massive in *Tripsacum lanceolatum* (3).

Peripheral stem bundles become progressively smaller and more reduced in successively lower internodes. This change is accompanied by an increase in their associated sheath sclerenchyma. Moreover, the walls of the fiber cells constituting the bundle sheath become thicker in successively lower internodes.

All plants of the race Zapalote chico conform to the structural pattern shown by the plant pictured in plate VII in that most of the peripheral bundles of upper internodes are connected to the epidermis by a sclerenchymatous bridge. A similar pattern, however, is not found in all races of maize. For bridging to occur in any plant internode it is necessary that the peripheral bundles lie close to the epidermis and that sufficient bundle sheath sclerenchyma develops at the phloem poles prior to the maturation of sub-epidermal tissue.

Papago has deep-lying peripheral bundles and though heavily sclerotic, none are bridged to the epidermis in any stem internode. Plants of the race Chapalote vary in their incidence of bridging, but the variation is correlative with peripheral bundle distance from the epidermis. On the other hand, proximity of peripheral bundles to the epidermis is not solely responsible for the incidence of bridging, either in a single stem or in a race. For example, peripheral bundles in all internodes of a teosinte stem lie close to the epidermis, but bridging only occurs in the peduncle and upper one or two internodes (plate X, A). In respect to races, all



peduncles of Zapalote chico plants studied have over fifty per cent of their peripheral bundles bridged to the epidermis, even when these bundles lie 150 microns from the epidermis (a distance greater than that of unbridged Chapalote plants). On the other hand, the peripheral bundles in the stems of Argentine pop lie relatively close to the epidermis, but are unbridged.

Considering only the phenomenon of bridging in maize, teosinte and *Tripsacum*, the following classification can be made.

1. *No bridging in any internode of the plant.* This condition is found in Argentine pop (plate IX; A, B) and in the North American pop corn race, Ladyfinger.
2. *Bridging in the tassel, tassel peduncle and 2-3 internodes below.* Northern flint, Zapalote chico (plate VII; A-F), Gourdseed (plate IX; C, D), Chapalote, and teosinte (plate X; A, B.)
3. *Bridging in all plant internodes.* *Tripsacum dactyloides* (plate X; C, D) and *Tripsacum lanceolatum*.

The lack of bridging in Argentine pop may be due to the distance of peripheral strands from the epidermis, paucity of sheath sclerenchyma, or both. It is possible, however, that it is in part a result of a particular pattern of growth, basically different from both *Tripsacum* and the races of maize which exhibit bridging. Argentine pop plants have a very slow growth rate and at maturity each plant consists of a great number of short internodes differing little in length (fig. 4). The longest internode occurs in the lower one-third of the plant. Beyond this point successive internodes gradually diminish in length up to the tassel peduncle, which itself is seldom longer than the internode next below and barely, if at all, exerted beyond the uppermost leaf sheath. Peripheral bundles are uniformly small and unstretched throughout the length of the plant. This infers that in each internode the peripheral bundles mature after the completion of tissue elongation. Hence, in all internodes of the stem, internodal tissue and peripheral bundles mature at a rather uniform rate, the former keeping ahead of the latter.

The presence of bridging in upper plant internodes but not in those below has been described for Zapalote chico (plate VII) and attributed to an extreme retardation in the rate of maturation of internodes above the ear shoots. A similar change occurs in the slow-maturing race Gourdseed, which like Zapalote chico, is characterized by a series of very short internodes between the ear and tassel.

Northern flint and teosinte grow rapidly and the upper internodes slow down only slightly in their rate of growth and maturation (fig. 4). As in Gourdseed and Zapalote chico, the peduncle and upper one or two internodes exhibit bridging. Such bridging is likely the result of a speeded-up maturation of peripheral bundles coupled with a slight decrease in stem tissue maturation, for the upper 2-3 leaves are always very much shorter than those below. Hence, the peripheral bundles have a much shorter distance to differentiate before reaching the stem. In the case of Zapalote chico, the change in peripheral bundle configuration is abrupt; in Northern flint and teosinte it is gradual. For example, in one plant of teosinte,



eighty percent of peripheral bundles in the peduncle were bridged to the epidermis, fifty percent in the internode below, fifteen percent in the next lowest internode and zero percent in the one below that.

In the genus *Tripsacum*, the formation of girder sclerenchyma is an outstanding feature of its strengthening system, occurring throughout the length of the plant (plate X; C, D). It is also a common structural arrangement in grasses generally. Hayward (1938) stated that stems so constructed have a "continuous zone of hypodermis variable in thickness within the epidermis and enclosing longitudinal bands of chlorenchyma". More precisely, the outer portion of such a stem consists of a parenchymatous cortex, regularly interrupted by girders of sclerotic tissue, which link peripheral bundles with the epidermis (plate X, C). Only in lower internodes do peripheral bundles become connected laterally by the sclerification of parenchyma lying between them (plate X, D). In these lower internodes the longitudinal bands of parenchyma appear to be "imbedded" in a continuous mass of hypodermal sclerenchyma, but actually, the isolation is circumscribed laterally by girder sclerenchyma and within by sclerified parenchyma. Percival (1921) stated that "a portion of the outer face of the chlorenchyma bands is always in immediate contact with the epidermis". This is true for the upper internodes of *Tripsacum* but in lower internodes the epidermis is underlain by a single layer of large hypodermal cells.

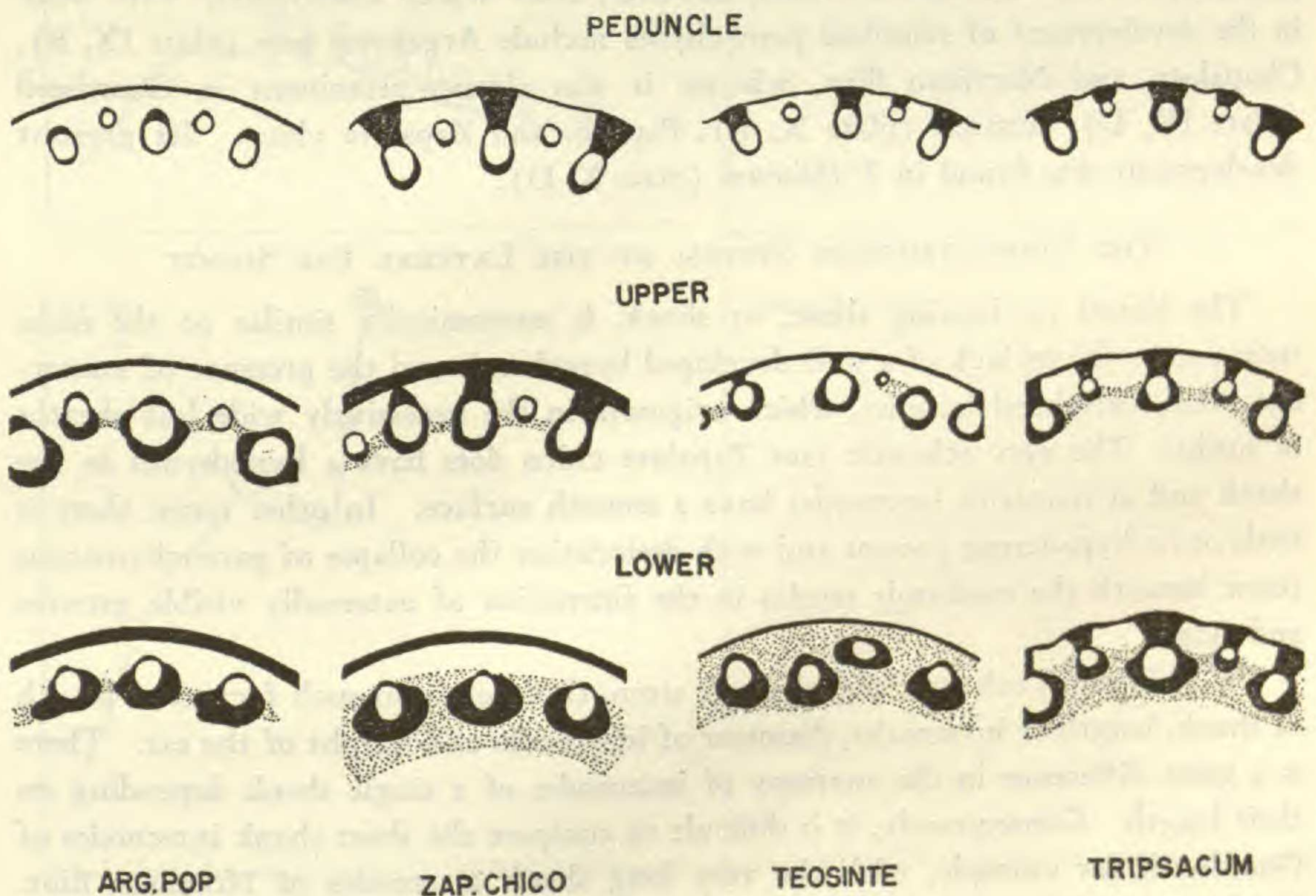


Fig. 3. Representative drawings of internodal cross-sections to show the variation in bridging within peduncle, upper internode, and lower internode in Argentine pop, Zapalote chico, Teosinte, and *Tripsacum*. Sclerotic fiber tissue in black; sclerified parenchyma stippled.



The peripheral bundles in *Tripsacum* lie close to the epidermis and their maturation in the stem either coincides with that of outer stem tissue or the procambium itself extends to the epidermis. *Tripsacum* has a rapid growth rate and at maturity consists of a relatively small number of extremely long narrow internodes culminating in an even longer peduncle (fig. 4). Maturation processes in this genus must be investigated before an attempt is made to compare its pattern of growth with maize.

In summary, the strengthening system found in the lower internodes of most maize races studied parallels the condition found in an entire Argentine pop plant. The upper internodes, however, have a structure resembling that of *Tripsacum*. Figure 3 diagrammatically represents the basic differences in bridging described in this section.

*Sclerified parenchyma.* In all plants examined the lower the internode the wider the zone of sclerified parenchyma. In lower internodes sclerified parenchyma forms a radially thick, sclerotic cylinder traversed by vascular bundles (plate VII, A). Higher up (approximately 8 internodes below the tassel peduncle) it is found chiefly between peripheral vascular bundles (plate VI, B; plate IX, B, D; plate X, B, D). In the fourth internode below the tassel peduncle interfascicular sclerenchyma is found only in Papago (plate VIII, A) and in the tassel peduncle sclerified parenchyma is never found (plate IX, A, C; plate X, A, C).

A high degree of intra-racial variation occurs in regard to the extent of parenchyma that becomes sclerified, however, races which consistently were weak in the development of sclerified parenchyma include Argentine pop (plate IX, B), Chapalote, and Northern flint, whereas it was always prominent in Gourdseed (plate IX, D), teosinte (plate X, B), Papago, and Zapalote chico. Its greatest development was found in *Tripsacum* (plate X, D).

#### THE STRENGTHENING SYSTEM OF THE LATERAL EAR SHOOT

The lateral ear-bearing shoot, or shank, is anatomically similar to the main stem except for its lack of a well-developed hypodermis and the presence of numerous small, peripheral bundles, which originate in the excessively wide leaf sheaths or husks. The very sclerotic race Zapalote chico does have a hypodermis in the shank and at maturity internodes have a smooth surface. In other races, there is little or no hypodermis present and with desiccation the collapse of parenchymatous tissue beneath the epidermis results in the formation of externally visible grooves and ridges.

In addition to sclerotic tissue, shank strength depends on such factors as length of shank, length of internodes, diameter of internodes and weight of the ear. There is a great difference in the anatomy of internodes of a single shank depending on their length. Consequently, it is difficult to compare the short shank internodes of Gourdseed, for example, with the very long shank internodes of Northern flint. Furthermore, the amount of sclerenchyma in a shank bearing a fertilized ear is much greater than in one which bears an unfertilized ear.



Vascular bundles in the shank are generally provided with a heavy sclerotic sheath, which frequently prevents crushing of vascular tissue when arching or bending occurs. The overall strength of the shank, however, depends on the strength of tissue between the bundles or the extent of ground tissue sclerification.

The races Zapalote chico and Papago, very sclerotic in respect to their stems, have a great amount of sclerified parenchyma in their shank internodes. In plants of these two races, shanks varied in length from 7–28 cm., but all were erect at maturity. Plants of the race Gourdseed characteristically have short shanks (6–16 cm.) and their internodes have a fair amount of sclerified parenchyma. Nevertheless, all shanks of this race were bent or broken due in large measure to the combination of a very heavy ear and narrow lower internodes.

Both Northern flint and Chapalote have relatively long shanks (11–32 cm.).

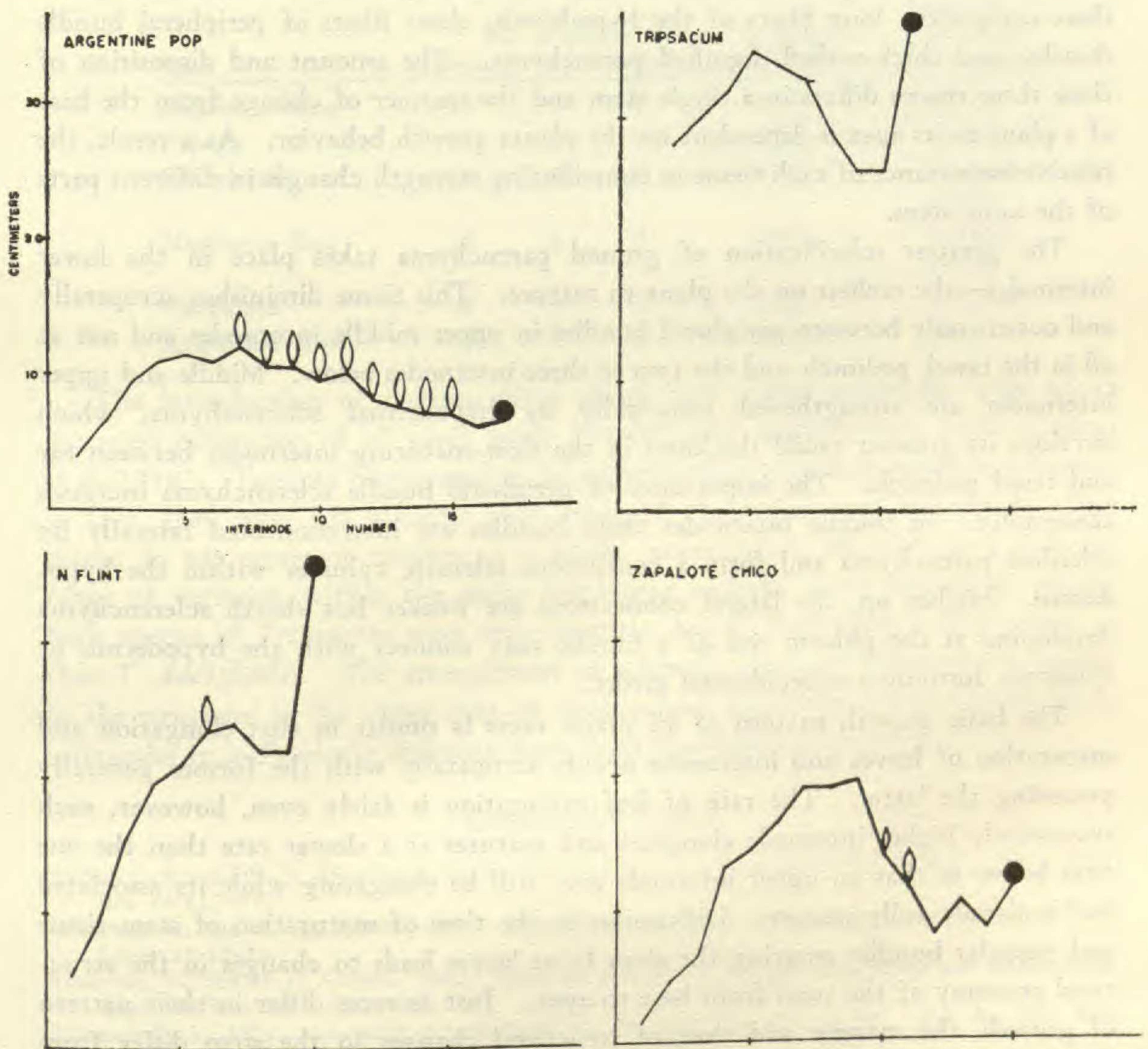


Fig. 4. Internode diagrams which typify the pattern of growth found in the races Argentine pop, Northern flint, and Zapalote chico, and the species *Tripsacum lanceolatum*.



At maturity all shanks of Chapalote plants were erect, whereas shanks of Northern flint plants were either bent or broken. The long shanks of Northern flint have few internodes and grow rapidly, while on the contrary, those of Chapalote have many internodes and a slow rate of growth. Anatomically, shank internodes of Chapalote have a wide zone of sclerified parenchyma, but there is practically none of this tissue present in the internodes of Northern flint. Since the stems of both races are quite similar in respect to sclerenchyma, the greater shank strength in Chapalote is probably due to the much longer period cells are able to deposit wall material before final maturation and desiccation.

Argentine pop has small ears borne on relatively short shanks which have many internodes, grow slowly and have fairly strong interbundle connections.

### CONCLUSION

The tissue which strengthens and supports a maize stem can be subdivided into three categories: long fibers of the hypodermis; short fibers of peripheral bundle sheaths; and thick-walled, lignified parenchyma. The amount and disposition of these three tissues differs in a single stem and the manner of change from the base of a plant to its apex is dependent on the plants growth behavior. As a result, the relative importance of each tissue in contributing strength changes in different parts of the same stem.

The greatest sclerification of ground parenchyma takes place in the lower internodes—the earliest on the plant to mature. This tissue diminishes acropetally and occurs only between peripheral bundles in upper middle internodes and not at all in the tassel, peduncle and the two to three internodes below. Middle and upper internodes are strengthened principally by hypodermal sclerenchyma, which develops its greatest radial thickness in the slow-maturing internodes between ear and tassel peduncle. The importance of peripheral bundle sclerenchyma increases acropetally. In middle internodes these bundles are interconnected laterally by sclerified parenchyma and form a continuous sclerotic cylinder within the hypodermis. Higher up, the lateral connections are weaker but sheath sclerenchyma developing at the phloem end of a bundle may connect with the hypodermis or epidermis forming a subepidermal girder.

The basic growth pattern of all maize races is similar in that elongation and maturation of leaves and internodes occurs acropetally with the former generally preceding the latter. The rate of leaf maturation is fairly even, however, each successively higher internode elongates and matures at a slower rate than the one next below so that an upper internode may still be elongating while its associated leaf is already fully mature. Differences in the time of maturation of stem tissue and vascular bundles entering the stem from leaves leads to changes in the structural anatomy of the stem from base to apex. Just as races differ in their pattern of growth, the manner and time of structural changes in the stem differ from plants of one race to those of another.



A race such as Argentine pop with a uniform rate of growth shows only slight changes in its structural anatomy from one internode to the next, whereas Zapalote chico with a rapid initial growth rate, which is abruptly slowed down above the position of an ear shoot, has a corresponding sudden change in structural anatomy. Northern flint with a rather even but rapid growth rate undergoes changes similar to those in Zapalote chico but much more gradually. In the upper internodes of such a plant the length of leaves decreases along with the time of stem maturation.

The maize races studied were classified for overall scleroticness on the basis of their hypodermis, peripheral bundle sheaths and sclerified parenchyma and the result was in agreement with field observations on standability. All plants used in the present study were harvested after final maturation and desiccation, at which time it was noted if stems were standing, bent over or broken. Results of this observation are presented below.

Race	No. of plants			% plants standing	Strength of stem based on anatomy
	standing	bent	broken		
Zapalote chico	14	1	0	93%	strong
Papago	13	2	1	87%	strong
Gourdseed	11	4	0	73%	medium strong
Northern flint	10	2	3	66%	medium strong
Chapalote	8	5	2	53%	medium
Argentine pop	3	7	5	20%	weak

The introduction of teosinte germ plasm into maize reportedly leads to an increased induration of all plant parts (Mangelsdorf and Cameron 1942; Galinat et al. 1956). Teosinte plants used in the present study were not especially indurate; in fact, they were less sclerotic than most of the maize races examined. Two plants do not represent teosinte as a whole; nevertheless, they do show that the range of variation within the genus *Euchlaena* includes quite unsclerotic plants. Both species of *Tripsacum* were very sclerotic, but *T. lanceolatum* much more so than *T. dactyloides*. The arrangement of sclerotic tissue in *Tripsacum* is similar to the structure in the upper part of teosinte and most maize races but in lower internodes it is distinctly different from both *Euchlaena* and maize.

#### LITERATURE CITED

- Anderson, E., and F. D. Blanchard. 1942. Prehistoric maize from Cañon del Muerto. *Amer. Jour. Bot.* 29:832-835.
- Anderson, E., and W. L. Brown. 1951. The standard exotics. *Maize Genetics Cooperation News Letter* 25:17-18.
- Anderson, E., and H. C. Cutler. 1942. Races of *Zea Mays*: I. Their recognition and classification. *Ann. Mo. Bot. Gard.* 29:69-88.
- Athanasoff, A. 1928. Anatomie et maturation des chaumes d'un pied de blé. *Ann. Sc. Nat. Bot.*, 10<sup>e</sup> série, t. x, p 1.
- Brown, W. L., and E. Anderson. 1947. The northern flint corns. *Ann. Mo. Bot. Gard.* 34:1-28.
- Brown, W. L., and E. Anderson. 1948. The southern dent corns. *Ann. Mo. Bot. Gard.* 35:255-268.
- Cutler, H. C., and M. C. Cutler. 1948. Studies on the structure of the maize plant. *Ann. Mo. Bot. Gard.* 35:301-316.



- Esau, K. 1943. Ontogeny of the vascular bundle in *Zea Mays*. *Hilgardia* 15:327-68.
- Evans, M. W., and F. O. Grover. 1940. Developmental morphology of the growing point of the shoot and the inflorescence in grasses. *Jour. Agric. Res.* 61:481-515.
- Farquharson, L. I. 1957. Hybridization of *Tripsacum* and *Zea*. *Jour. Heredity.* 48:295-299.
- Galinat, W. C., P. C. Mangelsdorf, and L. Pierson. 1956. Estimates of teosinte introgression in archaeological maize. *Bot. Mus. Leaflets, Harvard Univ.* 17:101-123.
- Hayward, H. E. 1938. *The Structure of Economic Plants*. Macmillan Company, New York.
- Hunter, J. W., and N. E. Dalbey. 1937. A histological study of stalk breaking in maize. *Amer. Jour. Bot.* 24:492-494.
- Kumazawa, M. 1940. On the vascular course of the leaf trace in *Zea Mays*; iii (In Japanese p. 503-504: English résumé.) *Bot. Mag. (Tokyo)* 54:493-504.
- Laubengayer, R. A. 1949. The vascular anatomy of the eight-rowed ear and tassel of Golden Bantam corn. *Amer. Jour. Bot.* 36:236-244.
- Ledin, R. B. 1954. The vegetative shoot apex of *Zea Mays*. *Amer. Jour. Bot.* 41:11-17.
- Lenz, L. W. 1948. Comparative histology of the female inflorescence of *Zea Mays*. *Ann. Mo. Bot. Gard.* 35:353-377.
- Magee, J. A. 1948. Histological structure of the stem of *Zea Mays* in relation to stiffness of stalk. *Iowa State Col. Jour. Sci.* 22:257-268.
- Mangelsdorf, P. C., and J. W. Cameron. 1942. Western Guatemala: a secondary center of origin of cultivated maize varieties. *Bot. Mus. Leaflets, Harvard Univ.* 10:217-252.
- Mangelsdorf, P. C., and R. G. Reeves. 1931. Hybridization of maize, *Tripsacum* and *Euchlaena*. *Jour. Heredity* 22:329-343.
- Percival, J. 1921. *The Wheat Plant*. E. P. Dutton Company, New York.
- Popham, R. A. 1951. Principal types of vegetative shoot apex organization in vascular plants. *Ohio Jour. Sci.* 51:248-270.
- Prat, H. 1935. Recherches sur la structure des chaumes. *Ann. Sc. Nat., 10<sup>e</sup> série, t. XVII:* 83-166.
- Reeves, R. G. 1950. Morphology of the ear and tassel of maize. *Amer. Jour. Bot.* 37:697-704.
- Wellhausen, E. J., Roberts, L. M., and Hernandez X., E., in collaboration with P. C. Mangelsdorf. 1952. Races of maize in Mexico. *Bussey Inst., Harvard Univ.*

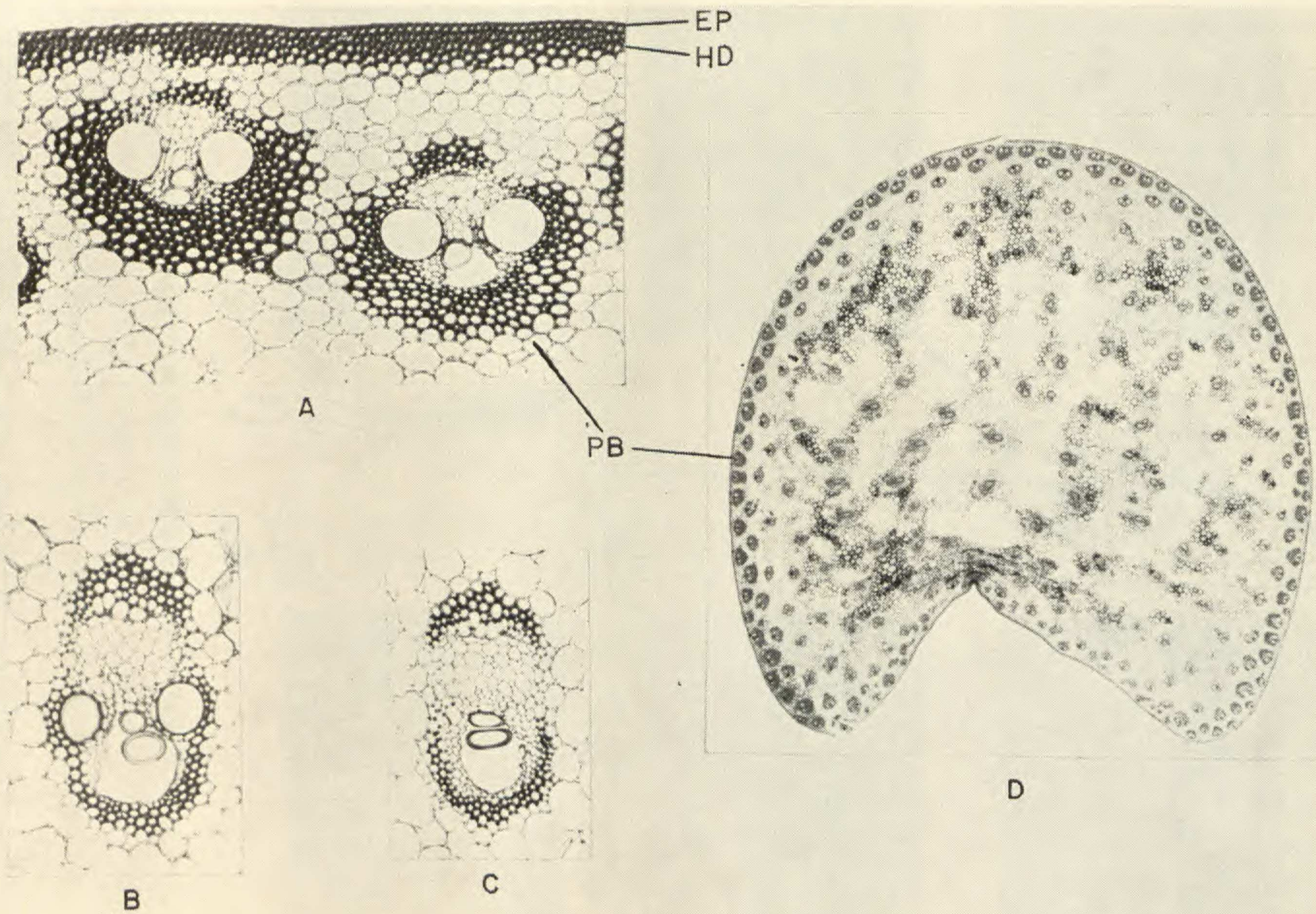
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### EXPLANATION OF PLATE

#### PLATE VI

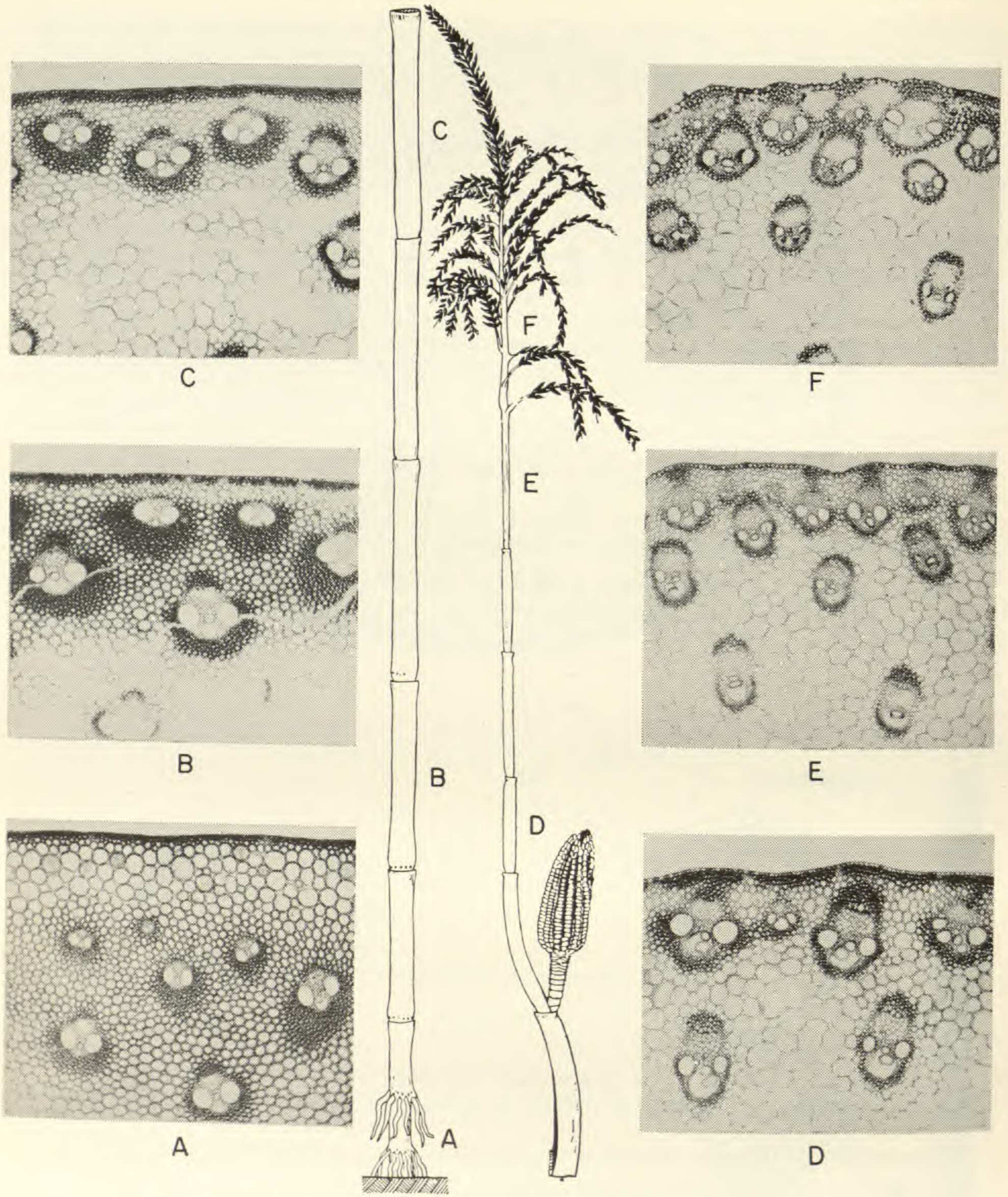
Structural features of a maize stem. A, Transection of the peripheral region of an internode showing hypodermis (HD), peripheral vascular bundles (PB), and thick-walled parenchyma between the latter ( $\times 100$ ). B, Transection of a vascular bundle ( $\times 107$ ). C, An atypical vascular bundle lacking well-developed metaxylem vessels. Bundles of this kind were found in the tassel peduncles of all Zapalote plants ( $\times 107$ ). D, Transection of a maize stem taken from a middle internode which shows the arrangement of vascular bundles ( $\times 7.7$ ).





MURDY—STRENGTHENING SYSTEM IN STEM OF MAIZE





MURDY—STRENGTHENING SYSTEM IN STEM OF MAIZE



## EXPLANATION OF PLATE

## PLATE VII

Scale drawing of a completely mature Zapalote chico plant with leaves removed ( $\frac{1}{7}$  natural size), and transverse anatomical sections from every third internode of this plant to show the changes in structural anatomy occurring in a single stem ( $\times 35$ ).



## EXPLANATION OF PLATE

## PLATE VIII

Transections of the fourth internode below the tassel peduncle to demonstrate racial differences in hypodermal development ( $\times 70$ ). A, Papago; B, Gourdseed; C, Chapalote; D, Northern flint; E, Teosinte.